Crown structure and leaf area index development in thinned and unthinned *Eucalyptus nitens* plantations

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Summary  The crown structure of *Eucalyptus nitens* (Deane & Maiden) Maiden 6 years after thinning, and the development of stand leaf area index both immediately and 6 years after thinning, were investigated. Thinning did not alter branch angle, branching density or the relationship between branch size and branch leaf area. However, larger branches were found in the lower crown of thinned trees and the increase in leaf area as a result of thinning occurred on the northern aspect of the crown. The vertical distribution of leaf area in unthinned trees was skewed toward the top of the crown and correlated with live crown ratio. The vertical distribution of leaf area in thinned trees tended to be less skewed and was unrelated to tree size or dominance. Leaf area index, as estimated from light interception measurements, increased at a constant rate soon after thinning regardless of residual stocking. In the longer term, residual stocking had a strong influence on leaf area increase per tree and was correlated with changes in crown length.

Keywords: branch angle, branch size, branching density, thinning, vertical leaf area distribution.

Introduction  Canopy size determines the productivity of forest stands through its role in radiation interception. Canopy size is often measured as leaf area index, which plays a key role in interception models (Jarvis and Leverenz 1983, Landsberg and Hingston 1996). Further, the structure of the crowns of individual trees also plays an important role in stand production through its effect on light penetration (Kellomäki et al. 1985) and canopy microclimate, including temperature, vapor pressure deficit and wind speed (Gary 1974). An understanding of both canopy size and structure is required to better understand and model growth.

Growth models in which radiation absorption is calculated on a stand basis commonly employ a horizontally continuous canopy of a given leaf area index (e.g., Linder et al. 1985, Landsberg and Hingston 1996). Though this approach is satisfactory for a closed canopy, it is less suitable for stands with a discontinuous or clumped canopy (e.g., thinned stands). A theoretical consideration of the influence of canopy structure using Beer’s law to describe light extinction throughout tree canopies showed that leaf area distribution can have an important effect on the amount of light absorbed (Larsen and Kernshaw 1996). Differences in canopy structure, such as canopy depth and foliar density, across a range of even-aged *Pinus contorta* var. *latifolia* (Engel.) Critch. stands were found to influence directly the amount and efficiency of stemwood production (Smith and Long 1989). Thus, the value of incorporating measures of foliage distribution into models of carbon gain has been recognized (McMurtrie et al. 1986, Whitehead 1986, Wang and Jarvis 1990, Whitehead et al. 1990).

High intensity thinning, as practiced in *Eucalyptus nitens* (Deane & Maiden) Maiden plantations in Tasmania, can change stand leaf area index dramatically. It is also likely that the discontinuous canopy resulting from thinning affects the radiation available to individual trees and may alter the structure of tree crowns and the stand as a whole. Changes in vertical distribution of foliage with changes in stand density or following thinning have been found in other tree species. Heavily thinned *Pinus radiata* D. Don trees had a greater proportion of foliage in lower sections of the crown than lightly thinned trees because of greater branch size and number (Siemon et al. 1980). An improvement in light conditions in the lower crowns of 24-year-old *Pseudotsuga menziesii* (Mirb.) Franco after thinning resulted in an increase in the foliage area of lower crown whors 7 years later (Brix 1981). Similarly, wider spacing induced a downward shift in relative foliage distribution in *P. menziesii*, with the effect more pronounced with increasing tree dominance (Maguire and Bennett 1996). However, some studies have found no difference in foliage distribution with thinning or stand density. A “normal” distribution of foliage was found for *Pinus resinosa* (Ait.) trees and stands despite differences in tree size and age, stand density and site quality (Stephens 1969). No effect of thinning or fertilization was found on the vertical distribution of foliage in *Pinus taeda* L. (Gillespie et al. 1994).

Although the vertical distribution of foliage varies widely among non-coniferous tree species (Jarvis and Leverenz...
1983), few studies have investigated the vertical distribution of foliage in Eucalyptus stands. A study of regenerating Eucalyptus maculata Hook. found the vertical distribution of leaf area was skewed to the top of individual tree crowns (Pook 1984), whereas in a coppiced plantation of Eucalyptus globulus Labill., the maximum amount of leaf area was found near the midpoint of the live crown (Pereira et al. 1987).

The objectives of the present study were to: (1) characterize the crown structure and vertical distribution of leaf area for mid-rotation (10- to 15-year-old) E. nitens plantations; (2) determine the effect of thinning on crown structure and vertical distribution of leaf area; and (3) quantify the rate of recovery of canopy leaf area following thinning.

Materials and methods

Site descriptions

Three E. nitens thinning trials were studied. The Goulds Country trial plantation was in northeast Tasmania (41°05′ S, 146°54′ E), 27 km northwest of the township of St. Helens, at an altitude of 120 m. The site previously carried Eucalyptus regnans F. Muell. native forest and has yellow podsolic soils formed on adamelite granites. The area was logged, burned and windrowed but no cultivation or chemical weed control was carried out before planting. The site was planted in 1984 with seedlings (Upper Toorongo provenance) at a spacing of 3.5 × 2.5 m (1143 trees ha–1). The plantation was fertilized in the first year with 180:80:0 kg ha–1 of N,P,K. There was no control of emergent woody weeds after planting. Mean annual rainfall is approximately 1000 mm. Mean daily maximum temperature is 6.8 °C.

The Creekton trial was in southeastern Tasmania (43°21′ S, 146°54′ E), 8 km southwest of Dover, at an altitude of 120 m. The site previously carried predominantly E. regnans with some Euca-

lyptus obliqua L’Hér. native forest and has fine sandy clay loam over clay gradational soils formed on Silurian-Devonian sandstone and siltstone. The site was logged in 1987, burned and windrowed but no cultivation was carried out before planting with seedlings of an unknown seedlot. Pre-planting herbicide (6 kg ha–1 atrazine plus 6 kg ha–1 amitrole) was applied 2 months before planting in 1987 at 3.0 × 2.4 m spacing (1389 trees ha–1). No fertilizer was applied. The site was planted in 1989 with seedlings of an unknown seedlot from the western distribution of E. nitens in Victoria at a 3.5 × 2.0-m spacing (1429 trees ha–1). A meteorological station was located approximately 500 m from the trial site. Mean annual rainfall is 1086 mm. The mean weekly maximum temperature is 19.5 °C and the mean weekly minimum temperature is 3.3 °C.

Crown structure

Measurements of crown structure were carried out on 16 trees destructively sampled from Goulds Country. Sampling was restricted to the 200 trees ha–1 and unthinned treatments. In the 200 trees ha–1 treatment, two trees were randomly selected from each of four diameter classes. Selection in the unthinned plots was limited to the best 200 trees ha–1. The best 200 trees ha–1 in the unthinned plots were identified when the trial was established by ranking trees based on stem size and potential merchantability class. The potential merchantability class was derived from a form assessment that used a categorical system for branching, stem form, defects and damage (Gerrand et al. 1997b). By limiting selection to the best 200 trees ha–1, comparisons between thinning treatments were based on trees that were of similar size and form before thinning. In the unthinned treatment, two trees were randomly selected from each of four diameter classes created from the best 200 trees ha–1.
Destructive sampling was carried out during the winter of 1997. Each tree was felled and the length from the top of the crown to the base of the lowest live branch divided into three zones. The diameters of all green branches were measured 40 mm from the main stem, as was the height of emergence on the main stem. The branch angle from the main stem was measured to the nearest five degrees, and the azimuth sector of each branch was recorded as either 1 (north to east), 2 (east to south), 3 (south to west) or 4 (west to north). A subsample of five branches was selected from each zone, representing the range of branch diameters present in the zone. Each of the sample branches was measured for total length. The leaves of each sample branch were then excised. A subsample of 10 leaves was taken, which represented the range of leaf size, age and thickness of the sample branch. The projected area of these leaves were measured with a leaf area meter (Delta-T Devices Ltd., Cambridge, U.K.). The remaining leaves from each sample branch were placed in a paper bag and dried at 35–40 °C for a minimum of 72 h before being placed in an 80 °C oven for 24 h. Subsamples measured for area were also dried. Dried bulk samples and subsamples were cooled over a desiccant and weighed. The weight and area measurements of the subsamples were used to calculate specific leaf area (cm² g⁻¹) for each branch. This figure was applied to the total bulk weight (bulk sample plus subsample) for each branch to estimate the leaf area.

Relationships predicting branch leaf area and branch length from branch cross-sectional area were derived by linear regression analysis. The relationships were applied to the measured diameters to calculate the leaf area and length of unsampled branches.

Assuming no curvature along the branch length, the stem height at each branch tip (Hₒ) was estimated as:

$$Hₒ = H_0 + \cos \theta L_{br},$$

where $H_0$ is height of branch emergence, $\theta$ is branch angle from the vertical and $L_{br}$ is branch length. The leaf area of each branch was distributed evenly at 0.1-m height intervals between $H_0$ and $H_c$. Crown length of each tree was divided into 0.1-m sections and branch leaf area within each section expressed as a proportion of total leaf area. These data were fitted to a two-parameter cumulative Weibull function using the NLIN procedure of the SAS software package (SAS Institute Inc., Cary, NC). The cumulative foliage distribution function took the form:

$$LA_x = \frac{LA\{\exp\left[-(x-w)/\beta\right]^\alpha - \exp\left[-(x+w)/\beta\right]^\alpha\}}{1 - \exp\left[-(1/\beta)^\alpha\right]},$$

where total tree leaf area (LA), the predicted leaf area ($LA_x$) within an interval of crown length having midpoint $x$ and a width of $2w$ can be estimated with Equation 3.

Crown volume was estimated by calculating the horizontal projection length of each branch at its maximum stem height, $H_c$. The stem height at which the maximum branch projection length occurred was identified. Thus the crown volume was estimated by summing the volume of two half-ellipsoids, each with a base area equal to the maximum crown projection area of the tree. The stem height at which the lowest green branch emerged defined the base of the lower ellipsoid.

Leaf area density (LAD) of each tree was calculated as the ratio of total leaf area to estimated total crown volume.

**Measuring stand leaf area index**

Measurements of leaf area index ($L'$) were made at Goulds Country, Lisle and Creekton with an LAI-2000 plant canopy analyzer (PCA, Li-Cor, Inc., Lincoln, NE). Readings were taken either under uniform, diffuse light conditions with 100% cloud cover, or at dawn and dusk. Three readings were taken from the four corners of each plot with a 270° viewcap to limit the reading to the plot. Understory exceeding 1.5 m in height was cleared to a distance of approximately 5 m from each plot corner. A sensor continuously recorded irradiances outside the plantation. This sensor (also with 270° viewcap) was rotated to take readings in the same direction as each of the readings inside the plantation.

Plot measurements of $L'$ at Lisle and Creekton were made 6 and 18 months after thinning. Plot measurements of $L'$ at Goulds Country were carried out during March 1997, 7 years after thinning, when the plantation was 13 years old. In each instance, output from the PCA was converted to an $L'$ value using a calibration factor developed for the *E. nitens* plantation in Tasmania (Cherry et al. 1998). The outer ring of the PCA was excluded from the $L'$ calculation to ensure that the reading was constrained to the plot. Thick understory in the Goulds Country trial made it necessary to limit measurements to one plot per thinning treatment. A regression of $L'$ to stand basal area was used to estimate $L'$ of the remaining plots. At Goulds Country, $L'$ immediately after thinning at Age 6 years was estimated by an allometric relationship between tree size and tree leaf area (Medhurst et al. 1999) and known tree sizes recorded at the time of thinning. The change in mean crown length at Goulds Country was calculated from crown lengths measured at Ages 7 and 13 years. Crown length was measured from a subsample of 100 trees ha⁻¹ in each plot. The change in...
leaf area per tree was calculated from $L^*$ estimates at Age 6 years and measurements at Age 13 years.

**Leaf area index of isolated trees**

The wide spacing and relatively small crowns of the 100 trees ha$^{-1}$ treatment at Lisle and Creekton meant that the plot corner method presented difficulties, because below-canopy readings close to that of the above-canopy readings can be rejected by the PCA (Li-Cor 1990). We therefore tested a single-tree sampling method at Creekton, which estimated $L^*$ from the crown projection area using the PCA measurement of LAD. The value of LAD is calculated by the PCA using a set of $x,y$ coordinates that describe crown shape and hence the length of crown “seen” by each of the five concentric rings. The crowns of trees at Creekton were assumed to be ellipsoids, in vertical cross section, so height to crown base, crown length and crown width were required to determine the $x,y$ coordinates for each of the five PCA viewing angles (Figure 1, after Acock et al. 1994). Measurements of LAD of isolated trees were carried out at Creekton on March 24, 1998. In the 100 trees ha$^{-1}$ plots, a reading was taken at the base of each tree in the north, south, east and west directions (using a 180° viewing cap to obscure operator and tree stem). Measurements were replicated three times. Total height, height to crown base and crown width in each of the four directions were measured for each tree.

Distances from crown base to the edge of the crown were calculated for each tree using the five angles of the PCA (7, 23, 38, 53 and 68°) and the assumptions of crown shape as described in Figure 1. A value of $L^*$ for the tree was obtained using only the fields of view of the PCA within the lateral extension of the crown.

Leaf area of each tree was estimated from the measurements of LAD and crown volume calculated by the PCA. The result was compared with leaf area estimated from tree diameter measurements made 12 months before the PCA measurements and an allometric relationship between *E. nitens* tree diameter and leaf area based on measurements in several plantations including that of Creekton (Medhurst et al. 1999).

**Data analysis**

Branch cross-sectional area (40 mm from the stem, $A_b$), branch length ($L_{br}$) and branch leaf area ($A_{lb}$) data were transformed using natural logarithms. A group linear regression procedure was used to determine the significance of thinning treatment and crown zone on relationships between the branch cross-sectional area, branch leaf area and branch length data. Correction coefficients for back-transformation bias in logarithmic models were calculated by the method of Snowdon (1991). Differences in specific leaf area (SLA) between treatments and crown zones were tested by analysis of variance.

Differences in branch arrangement between thinning treatments were analyzed by unpaired $t$-tests. Differences within trees were analyzed by paired $t$-tests. The change in stand $L^*$ at Lisle and Creekton was analyzed by regression analysis.

**Results**

**Branch structure**

The relationship between branch cross-sectional area ($A_b$) and branch length ($L_{br}$) was independent of thinning treatment ($P > 0.05$). However, the slope and the intercept were influenced by crown zone ($P < 0.05$, Table 1). There was little overlap in $A_b$ values between crown zones. In the upper zone, 75% of branches were less than 11 mm in diameter, whereas only 25% of branches in the lower zone were less than 30 mm and the smallest branch diameter measured in the lower zone was 18 mm. The correction coefficient for back-transformation bias of the logarithmic model was 1.05.

There was a common slope across thinning treatments and canopy zones for the relationship between $A_b$ and branch leaf area ($A_{lb}$). However, although the intercept of the relationship was common between branches from thinned and unthinned trees, it was necessary to use a different intercept for each canopy zone ($P < 0.01$, Table 2). The branches of the lower zone had the lowest intercept, so when the model was back-transformed, branches in this zone had a smaller leaf area for a given branch cross-sectional area compared with the other zones. The correction coefficient for back-transformation bias of the logarithmic model was 1.08.

The proportion of branches in each crown zone of thinned and unthinned trees was similar ($P > 0.05$). On average, 16% of branches were found in the lower third of the crown, 32% in the middle crown and 52% in the upper crown. Consequently, the branching density of each crown zone was similar for thinned and unthinned trees ($P > 0.05$) with a mean of 2.9 branches m$^{-1}$ of stem height in the lower, 5.8 branches m$^{-1}$ in the middle, and 9.4 branches m$^{-1}$ in the upper zone.

Significantly larger branches were found in the lower crown zone of thinned trees when compared with unthinned trees ($P < 0.05$). Similar branch sizes were found in the middle and upper crown zones across thinning treatments.

A similar proportion of branches was found on the northern (51%) and southern (49%) aspects of thinned and unthinned trees ($P > 0.05$). The branches on the northern aspect of thinned trees were significantly larger than the branches on the...
Branch angle from the vertical increased with crown depth. Mean branch angle was positively correlated to tree diameter at breast height in the middle and lower crown zones (P < 0.01, Figures 2b and 2c), but no relationship was found for the branches in the upper crowns (P > 0.05, Figure 2a). Thinning did not significantly affect mean branch angle in any of the three crown zones (P > 0.05).

Within-tree leaf area distribution
Thinned and unthinned trees had similar amounts of leaf area in each of the lower, middle and upper crown zones in the southern aspect (P > 0.05). In the northern aspect, thinned trees had greater amounts of foliage in the lower and middle crown zones (P < 0.05, Figures 3a–d). Specific leaf area (SLA) decreased with increasing crown height (P < 0.01) but no significant difference was found between the thinning treatments (P = 0.06).

The Weibull model provided an adequate fit of the vertical leaf area distributions for both thinned and unthinned trees (Figures 4a and 4b). The α parameter was correlated with tree size in the unthinned treatment, with smaller trees having more foliage toward the top of the crown (Table 3). The α parameter showed no clear relationship with tree size in the thinned treatment. A strong relationship between the live crown ratio (ratio of green crown length to total tree height) and α was found for unthinned trees (Figure 5).

The assumptions about crown shape provided a reasonable estimate of crown volume (Figures 6a and 6b). Tree LAD was independent of tree size. The mean LAD of thinned trees was 0.91 m² m⁻³ whereas the mean LAD of unthinned trees was 1.04 m² m⁻³. This difference was not statistically significant (P > 0.05, t-test).

Stand leaf area index measurement
Leaf area indices (L*) increased at a similar rate for all thinning treatments at Lisle during the first 18 months after thinning (Table 4). Values of the L* of the unthinned treatment did not change during this period. Each thinned treatment increased L* by approximately 0.5 m² m⁻² during the 6–18 months after thinning. At Creekton, L* increased in the 18 months after thinning in the 250 trees ha⁻¹, 600 trees ha⁻¹ and unthinned treatments. The L* of the 100 trees ha⁻¹ treatment did not

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Table 1. Values of parameters for a linear regression model to predict the natural logarithm of branch length (Lb) as a function of the natural logarithm of branch cross-sectional area (Ab) by crown zone (i), ln(Lb) = (A + ai) + (B + bi)ln(Ab), for thinned and unthinned trees at Goulds Country. Standard errors of parameters are in parentheses. The coefficient of determination (r²) for the model was 0.95.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Effect</th>
<th>Details</th>
<th>Parameter value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>Mean (A)</td>
<td>i = Lower zone</td>
<td>−1.69 (0.06)</td>
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<tr>
<td>Zone (ai)</td>
<td>i = Middle zone</td>
<td>0.41 (0.16)</td>
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</tr>
<tr>
<td>i = Upper zone</td>
<td>0.14 (0.09)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Slope</td>
<td>Mean (B)</td>
<td>i = Lower zone</td>
<td>0.43 (0.01)</td>
</tr>
<tr>
<td>Zone (bi)</td>
<td>i = Middle zone</td>
<td>−0.07 (0.02)</td>
<td></td>
</tr>
<tr>
<td>i = Upper zone</td>
<td>−0.04 (0.02)</td>
<td></td>
<td></td>
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</tbody>
</table>

Table 2. Values of parameters for a linear regression model of the natural logarithm of branch leaf area (Ab) as a function of the natural logarithm of branch cross-sectional area (Ab) by crown zone (i), ln(Ab) = (A + ai) + Bln(Ab), for thinned and unthinned trees at Goulds Country. Standard errors of parameters are in parentheses. The coefficient of determination (r²) for the model was 0.91.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Effect</th>
<th>Details</th>
<th>Parameter value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
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<td>i = Lower zone</td>
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</tr>
<tr>
<td>Zone (ai)</td>
<td>i = Middle zone</td>
<td>−0.61 (0.10)</td>
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<tr>
<td>i = Upper zone</td>
<td>0.20 (0.09)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Slope</td>
<td>Mean (B)</td>
<td>1.18 (0.03)</td>
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</table>
change during this period (Table 4).

At Goulds Country, $L^*$ varied with stocking density ($P < 0.01$) (Figure 7a). Six years after thinning (i.e., at Age 13 years), $L^*$ increased with stocking from 1.47 (100 trees ha$^{-1}$) to 4.32 in the unthinned treatment (725 trees ha$^{-1}$). The percentage increase in $L^*$ after thinning declined with increasing residual stocking from 220% for the 100 trees ha$^{-1}$ treatment to 117% for the unthinned treatment. The change in leaf area per tree was strongly related to the intensity of thinning (Figure 7b).

The change in leaf area per tree in the thinned treatments was associated with an increase in crown length (Figure 8). The change in leaf area per tree in the unthinned treatment was less strongly related to change in crown length.

Leaf area index – isolated tree measurement

Out of 24 trees measured at Creekton in the 100 trees ha$^{-1}$ treatment, only one had a crown base so low (4.1 m) that two rings (7 and 23°) could be used to calculate leaf area. This was the only tree with an estimated leaf area greater than that calculated using residual stocking from 220% for the 100 trees ha$^{-1}$ treatment to 117% for the unthinned treatment. The change in leaf area per tree was strongly related to the intensity of thinning (Figure 7b).

The change in leaf area per tree in the thinned treatments was associated with an increase in crown length (Figure 8). The change in leaf area per tree in the unthinned treatment was less strongly related to change in crown length.

Table 3. Weibull parameter estimates for crown leaf area distribution by thinning treatment. 95% confidence intervals are shown in parentheses. Abbreviation: DBH is diameter at breast height.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>DBH (cm)</th>
<th>$\alpha$</th>
<th>$\beta$</th>
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<tr>
<td>Thinned</td>
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</tr>
<tr>
<td>23.4</td>
<td>3.195 (3.144–3.245)</td>
<td>0.545 (0.543–0.547)</td>
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<tr>
<td>25.9</td>
<td>2.628 (2.608–2.648)</td>
<td>0.571 (0.570–0.573)</td>
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<tr>
<td>28.0</td>
<td>2.710 (2.680–2.740)</td>
<td>0.479 (0.478–0.480)</td>
<td></td>
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<tr>
<td>30.1</td>
<td>2.709 (2.693–2.726)</td>
<td>0.564 (0.563–0.565)</td>
<td></td>
</tr>
<tr>
<td>30.6</td>
<td>3.024 (2.997–3.052)</td>
<td>0.492 (0.491–0.494)</td>
<td></td>
</tr>
<tr>
<td>34.7</td>
<td>2.274 (2.250–2.297)</td>
<td>0.477 (0.475–0.478)</td>
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<tr>
<td>34.2</td>
<td>2.511 (2.492–2.530)</td>
<td>0.539 (0.538–0.540)</td>
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<tr>
<td>38.7</td>
<td>2.473 (2.442–2.504)</td>
<td>0.553 (0.551–0.555)</td>
<td></td>
</tr>
<tr>
<td>Unthinned</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>16.4</td>
<td>2.441 (2.400–2.483)</td>
<td>0.558 (0.556–0.561)</td>
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<tr>
<td>17.9</td>
<td>2.012 (1.964–2.059)</td>
<td>0.458 (0.455–0.462)</td>
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<tr>
<td>21.8</td>
<td>2.159 (2.134–2.183)</td>
<td>0.445 (0.444–0.447)</td>
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<tr>
<td>23.3</td>
<td>2.477 (2.446–2.507)</td>
<td>0.461 (0.460–0.463)</td>
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<tr>
<td>25.8</td>
<td>2.651 (2.633–2.670)</td>
<td>0.540 (0.539–0.541)</td>
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<tr>
<td>30.3</td>
<td>2.718 (2.696–2.741)</td>
<td>0.487 (0.486–0.488)</td>
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<tr>
<td>34.7</td>
<td>2.554 (2.527–2.582)</td>
<td>0.485 (0.483–0.486)</td>
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</tr>
<tr>
<td>34.9</td>
<td>2.832 (2.809–2.854)</td>
<td>0.528 (0.527–0.529)</td>
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</table>

Figure 3. The distribution of leaf area (m$^2$ tree$^{-1}$) and range of specific leaf area (m$^2$ kg$^{-1}$) for the upper, middle and lower parts of the crown of thinned (a and b) and unthinned (c and d) trees. Panels (a) and (c) show the northern aspect of the crown, panels (b) and (d) show the southern aspect.

Figure 4. Examples of vertical leaf area distribution for (a) a thinned and (b) an unthinned tree at Goulds Country. Dotted lines show fitted Weibull function.

Figure 5. Relationship between live crown ratio and the $\alpha$ parameter of the Weibull function (shape of the vertical foliage distribution) for thinned and unthinned trees at Goulds Country. Closed symbols represent thinned trees and open symbols represent unthinned trees. The regression line is fitted only to the unthinned data.
calculated 12 months previously from the allometric relationship with breast height diameter (Figure 9). The height to crown base measures of the remaining trees were all greater than 4.1 m and the PCA calculation of LAD was confined to measurements made with only the 7th ring. The isolated tree measurements in low density *E. nitens* stands probably yielded an underestimate of stand $L^*$ and hence the plot corner method was preferred for estimating $L^*$.  

**Discussion**

**Branching structure**

This study has shown that branch size, and hence crown size, can be manipulated through thinning treatment. However, the basic elements of crown structure such as branching density, angle and orientation were unaffected by thinning. The environment in which a tree grows can affect branch properties. For example, large differences in branch angle were noted between open-grown and shaded trees for several Tasmanian rainforest species, including *Nothofagus cunninghamii* (Hook.) Oerst. and *Atherosperma moschatum* Labill. (King 1998). Such differences are likely a result of the ability of shade-tolerant species to alter branching patterns in response to irradiance, in order to maximize light interception. It is possible that shade-intolerant species such as *E. nitens* (Boland et
Branch leaf area increased strongly with branch size, but the rate of increase declined with crown depth regardless of thinning (Table 2). Similar patterns of leaf area display have been found in other studies of *E. nitens* (Battaglia et al. 1998, White et al. 1998). Similar changes in this relationship were found in *P. taeda* but differences with crown depth narrowed after fertilizer treatment, suggesting that the decline was a result of N limitation as well as low irradiance (Gillespie et al. 1994). The value of $L^*$ of mature canopies of *E. nitens* generally increases following application of N fertilizer (P. Smethurst, CSIRO/CRC-SPF, unpublished data). Further research is required to determine if this is because of an increase in branch size or a change in the relationship between branch size and branch leaf area with crown depth.

Thinning resulted in larger branches in the lower section of the crown. If thinning is carried out before the live crown has risen beyond a specified height, large branches can degrade wood quality if pruning is not implemented. Silvicultural regimes developed for *E. nitens* sawlog plantations incorporate a pruning system that ensures the production of knot-free wood in the first 6 m of the stem from its base (Forestry Tasmania 1999).

**Vertical distribution of leaf area**

The vertical distribution of leaf area of the unthinned *E. nitens* trees was skewed toward the top of the crown of individual trees, but there was a shift toward a normal distribution with increasing dominance. In a closed canopy, differences in light availability are inevitably associated with tree height, and more suppressed trees show an upward shift in vertical leaf area distribution compared with more dominant trees (Maguire and Bennett 1996, Xu and Harrington 1998). Once *Eucalyptus* stands reach canopy closure, $L^*$ often declines (Beadle et al. 1995). This decline is generally attributed to a loss of leaf area from the base of the tree crowns because of low irradiance (Mäkelä and Vanninen 1998). The loss of leaf area might be expected to cause a redistribution of leaf area toward the top of the canopy. High intensity thinning of a stand either before or after canopy closure sustains or improves the light environment of the lower crown, and a less-skewed leaf area distribution in the crowns of thinned trees might be expected. In this study, the improved light conditions after thinning resulted in the retention and continued growth of live branches at the base of the crown. This shifted the vertical distribution of leaf area toward a normal distribution and differences in relative dominance were reduced because of the openness of the canopy. These distributions were similar to those of thinned and unthinned *Pinus contorta* Dougl. where the foliage of unthinned trees was displaced toward the crown top (Gary 1978). As leaf area distribution in thinned trees was not related to dominance, the more normal distribution of leaf area may reflect the optimal leaf area distribution for an individual *E. nitens* tree. A leaf area distribution with a downward shift toward the crown base of the layer with maximum leaf area may maximize light harvesting and minimize self-shading (Kellomäki and Wang 1997).
As with other tree species (Vose 1988, Mori and Hagihara 1991), the Weibull function provided a realistic description of vertical leaf area distribution of mid-rotation trees. Thinning shifted the shape of this distribution toward normal and, because of the lack of correlation with tree size, mean value of α and β parameters could be used to describe vertical leaf area distribution in canopy models. The vertical profile of unthinned trees in closed-canopy stands was not normally distributed and appears to be related to relative dominance. The use of average parameters for unthinned crowns is, therefore, not recommended. However, the use of the Weibull model may be valid in describing the vertical leaf area distribution of the entire canopy.

Differences in horizontal distribution of leaf area were not examined as part of this study but may exist between thinning treatments. However, stand density and $L'$ had no influence on horizontal distribution of foliage in P. taeda, suggesting that within-crown light distribution determines this structural feature rather than the light environment of the canopy as a whole (Xu and Harrington 1998).

$L'$ development

The observed $L'$ values for the fully closed, unthinned canopy at each of the three sites were in the range of those reported for Eucalyptus stands (Linder 1985, Beadle 1997). The initial increases in $L'$ following thinning (Table 4) were generally independent of residual stocking but in the longer term, the rate of change in $L'$ was higher in the more heavily thinned treatments (Figure 7a). Although absolute changes in $L'$ were similar across all thinning treatments, the relative rate of increase was much greater for the stands of lower stocking. This may be because of a higher proportion of assimilated carbon being allocated to canopy development in these widely spaced stands (Bernardo et al. 1998). Leaf area density was not changed by thinning due to similar branch angle, branch cross-sectional area–length, and branch cross-sectional area–leaf area relationships. As thinning did not alter LAD and as crown width will eventually be constrained by mechanical support requirements, maximum leaf area of a tree may be determined by the maximum crown length a site can support. Therefore, if maximum crown length and width at a site are known, a maximum leaf area per tree can be estimated and the minimum residual stocking that can regain the site’s maximum $L'$ can also be estimated.

For thinned stands, the change in leaf area per tree was strongly related to the change in mean crown length (Figure 8). Change in tree leaf area is a function of both change in crown width and change in crown length. However, the change in crown length appears to be the stronger driving variable in these stands, because the change in crown width will ultimately be constrained by structural support requirements. The unthinned treatment showed less of a relationship between change in mean leaf area per tree and change in mean crown length. The change in mean crown length may be overestimated for this treatment because, of the 100 trees ha$^{-1}$ sub-sample measured for total height and crown length, 50 trees ha$^{-1}$ were the dominant trees in the treatment. Thus the true mean change in crown length for the unthinned stand may be much lower.

Conclusions

Results from this study have described the effect of thinning on branch size and distribution, crown shape and canopy development. A move toward uniform vertical leaf area distribution with increase in inter-tree spacing was observed. This implies that simple assumptions about the interception and attenuation of light can be made on an individual tree basis for heavily thinned or widely spaced stands. However, despite relatively large increases in $L'$ after thinning, heavily thinned stands are unlikely to return to full canopy closure. The crown structure and leaf area relationships described in this paper can be used to calculate the light interception of trees in stands that have been heavily thinned. The Beer–Lambert law for estimating light attenuation is more appropriate for closed canopies. Thus, tree growth models that consider light interception as a function of crown size and shape will be most suited to accurately reflect the conditions of a thinned stand and provide good predictions of growth (e.g., Courbaud 2000).

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